



REVIEW ARTICLE

# Metabolomics studies on Solanaceae members under abiotic stress: A review

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## Abstract

Plants are known to face various abiotic stresses, which lead to reduced yield. It has been reported that metabolite concentrations vary under different abiotic stress conditions. Metabolomic studies are widely used to analyse the compositions of various metabolites. Metabolomic studies utilise different methods such as gas chromatography (GC), liquid chromatography (LC) in combination with mass spectrometry (MS) and nuclear magnetic resonance (NMR) to analyse metabolites. The complete set of low-molecular weight metabolites present in the cell constitutes the metabolome. The amino acid proline is a major metabolite present in most stressed plants. Plant tissues exhibit altered amino acid and sugar levels under stress. As with other plant groups, similar responses are observed in members of the Solanaceae family. When solanaceous plants are subjected to stress, their cell activates the antioxidant systems to eliminate reactive oxygen species (ROS) produced in response to stress. Reactive oxygen species are scavenged by enzymatic antioxidants such as superoxide dismutase (SOD) and peroxidase (POD), as well as by non-enzymatic antioxidants, including flavonoids and ascorbic acid.

**Keywords:** abiotic stress; metabolomics; Solanaceae

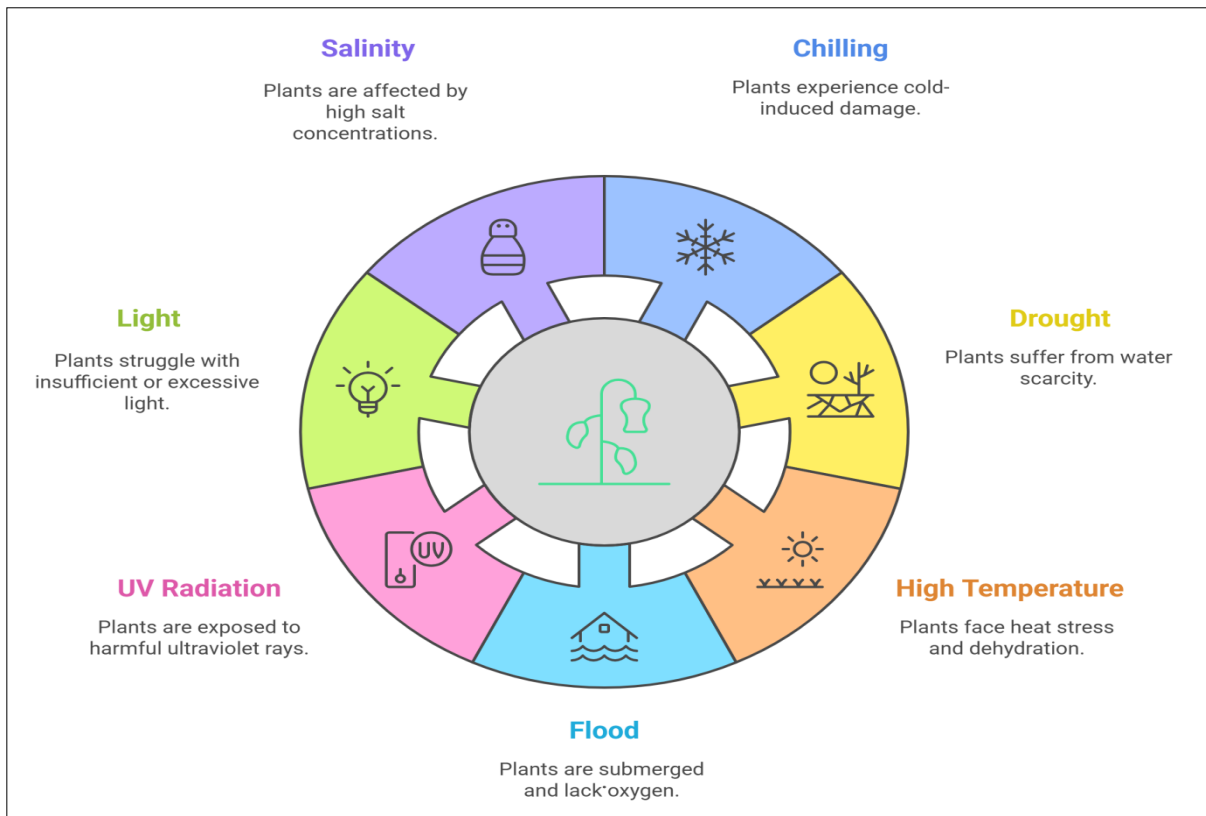
## Introduction

After Poaceae and Fabaceae, Solanaceae is the most economically important plant family. It includes a wide range of economically important vegetable crops, such as potato, tomato, eggplant and pepper. After wheat, corn and rice, the output of potatoes ranks fourth globally (1). The family comprises 90 genera, each with 3000–4000 species. The family includes perennial trees and annual herbaceous plants and occurs in a variety of terrestrial habitats, including rainforests and deserts (2). Members of the Solanaceae family are rich in carbohydrates, fats, proteins, vitamins, minerals and other essential nutrients, including flavonoids and phenols, which help protect against stress and degenerative diseases (3). The Solanaceae family typifies ethnobotany, or extensive human use of plants. It is a significant source of spices, food and medicine (4). Within the family Solanaceae, in addition to crops, several medicinal plants are used for alkaloid production, e.g., jimsonweed, deadly nightshade and black henbane (5).

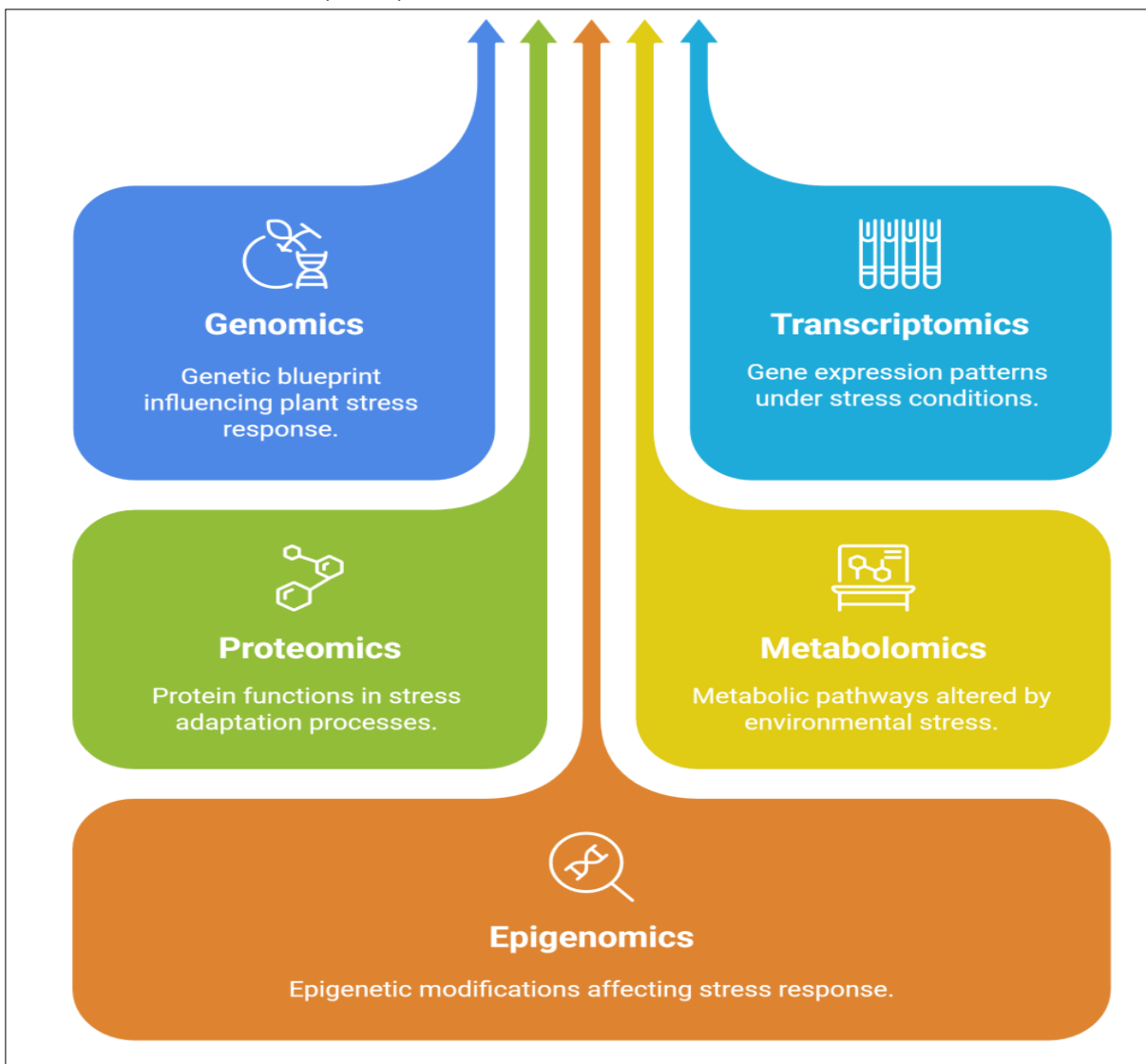
Plants require specific environmental conditions for optimal growth. Various abiotic factors affect plants differently depending on their quantity or intensity. Any deviation from ideal environmental conditions, such as a surplus or shortfall in physical or chemical factors, is referred to as abiotic stress and has been shown to be detrimental to plant development, growth and production. However, the environments in which plants live are

constantly changing and often adverse to their growth and flourishing. Abiotic stressors such as drought, heat, cold and salinity are examples of these unfavorable conditions. Salt, temperature and drought are the primary abiotic stressors that influence the geographic distribution of plants in nature, limit agricultural yields and jeopardize food security (6). Abiotic stress tends to erode a plant's defenses, making it more susceptible to viral and pest attacks. Abiotic stressors affect plants' growth and productivity (Fig. 1). Therefore, how they respond to these stresses is important for their ability to adapt to environmental change and survive (7). Plants react dynamically and intricately to abiotic stressors by altering their molecular, cellular and physiological makeup. Now that the genomes of numerous plant species have been sequenced, the pursuit of functional genomics has significantly accelerated the emergence of other omics, such as metabolomics (Fig. 2). Even though many metabolites remain to be identified, metabolomics has made a substantial contribution.

Over the years, attempts have been made to both improve understanding and the development of plant biology from the perspective of the small compounds produced by biological processes and to enhance plant behavior in both ordinary and stressful environments (8). The quantity and diversity of metabolites produced by plants are essential for their growth, development and adaptation to their environment. The many small-molecule metabolites that underpin crop quality and



**Fig. 1.** Various abiotic stresses and their impact on plants.



**Fig. 2.** The schematic illustration of various integrated “omics” approaches to analyse the plant responses to abiotic stresses.

productivity serve as significant sources of food and energy for all living organisms, including humans (9). Primary and secondary metabolites may generally be distinguished from these compounds. The latter, but not the former, are essential for a plant to survive under harsh conditions by maintaining a delicate balance with its surroundings. Also, while secondary metabolite abundances and structures vary greatly across plant kingdoms, primary metabolite abundances and architectures are highly conserved (10).

The methods and tools used in plant Metabolomics to completely identify, quantify and localise each molecule are crucial to the outcomes. Due to the intricacy of the various metabolic features and chemical abundances, it is an exceedingly difficult task. Fortunately, although it currently appears difficult to accurately and thoroughly analyse the entire metabolome of a biological sample, methods and equipment for plant metabolomics have been evolving rapidly (11). This large-scale analysis is made possible by several integrated technologies and approaches, including and mass spectrometry (MS) based techniques such as Gas chromatography mass spectrometry (GC-MS), Liquid chromatography mass spectrometry (LC-MS), Capillary electrophoresis-MS (CE-MS), Fourier transform ion cyclotron resonance-MS (FT-ICR-MS), non-destructive nuclear magnetic resonance (NMR) spectroscopy (12, 13).

The mannitol, sorbitol and dimethylsulfonium compounds, such as glycine betaine and dimethylsulfoniopropionate, sugars like sucrose and fructan, or amino acids like ectoine and proline and glycoalkaloids (GAs) like solanine chaconin, solasonine, solamargine and tomatine that act as osmolytes and osmo-protectants to shield plants from excessive drought, salt and desiccation are a few examples of plant metabolites (14). There are reports about the large-scale production of steroidal alkaloids (SAs) and their glycosylated forms (SGAs) in the members of Solanaceae under abiotic stress conditions. According to reports, SGAs in the cytosolic mevalonic acid pathway are derived from acetyl-CoA (15). Improving our understanding of the SAs biosynthesis pathway, the subcellular transport of these molecules and the regulatory and signalling factors linked to SA metabolism will probably help members of this economically significant family better understand how they tolerate abiotic stress. Additionally, this kind of study will provide tools to develop crops with altered levels of SAs through genetic engineering or traditional breeding.

Different epicuticular waxes function as mechanical barriers to pathogens and protect plants from excessive water loss during drought. The degree of saturation of membrane fatty acids can significantly affect cold tolerance. Numerous small molecules protect plants from oxidative damage caused by various stressors. Glutathione (GSH), anthocyanins, ascorbic acid, tocopherols and carotenoids, which remove active oxygen intermediates, protect plant tissues from oxidative stress. The general phenylpropanoid pathway is activated during plant defense responses and phytoalexin production and lignin biosynthesis are also induced. Small molecules produced in response to stress, such as jasmonic acid (JA), methyl jasmonate, salicylic acid (SA) and methyl salicylate, can also serve as chemical messengers that trigger systemic defense and acclimation responses (16). In this review, we summarize our current understanding of the metabolome under abiotic stresses, including drought, waterlogging, salinity and high and low temperatures, in the Solanaceae family. The

metabolomic investigations and methods used to elucidate the mechanisms of abiotic stress tolerance in members of the Solanaceae family are summarised in Table 1.

## A brief account of common techniques used in metabolomics studies

### Gas chromatography mass spectrometry

Gas chromatography mass spectrometry (GC-MS) is the most established metabolomics technology. In it, a chromatographic method is used to separate the complex mixture and a mass spectrometer (MS) also provides chemical and structural information (15).

Volatile and thermostable compounds can be separated only by gas chromatography and other polar metabolites must be derivatised to become volatile (16). Based on thermodynamic properties, components get separated in GC. A mass analyser follows GC. Before entering the mass analyser, components are converted into charged particles by using various methods, such as electron impact and electrospray ionisation. Determining the mass-to-charge ratio of ions is the fundamental goal of MS. The mass analyser separates charged ions based on their mass-to-charge ratio. All types of mass analysers, including ion traps, single quadrupoles, time-of-flight (TOF) and magnetic mass spectrometers, operate on different principles. The time-of-flight analyser offers high scanning speed, has higher ion-collection efficiency and achieves a resolution of up to 40000 (15). The mass analyser then generates 3D information on the target compound. Gas chromatography is widely used for metabolite profiling. Databases such as the National Institute of Standards and Technology are used for the annotation of GC-MS peaks (17).

The literature reports a study in which GC-MS-based analysis of methanolic or ethanolic extracts of salt-stress-induced callus tissue of *Solanum melongena* L. showed the presence of secondary metabolites such as alkaloids, saponins, steroids, tannins/phenolics, flavonoids, glycosides and reducing sugars (44). Another study reports the variation of endogenous hormone profile of the Solanaceous plants under salinity stress. In this GC-MS-based metabolomics study, it is revealed that crosstalk between endogenous hormones plays an important role in abiotic stress response (45).

Studies on metabolites associated with chilling tolerance of tomato fruit pericarp (*Solanum lycopersicum* L. cv. Micro-Tom) using GC-MS metabolite profiling reports 363 analytes from fruit pericarp of which 65 are reported to be metabolites (46). Increased production of volatile terpenoids was reported in tomato by researchers using SPME-GC-MS studies (47). Gas chromatography mass spectrometry is cheaper as compared to the other techniques, but it is limited to thermo-stable and volatile compounds.

The use of GC-MS in metabolomics investigations of members of the Solanaceae has been documented extensively. Table 1 compiles the reports on common techniques used for the metabolomics studies of Solanaceae members under abiotic stress.

### Liquid chromatography mass spectrometry

The mobile phase in liquid chromatography mass spectrometry (LC-MS) is liquid that is passed through the column containing the stationary phase which resists the flow of the liquid. High pressure is required to make the mobile phase rapidly flow in the column. It does not involve any derivatisation process, i.e. there is no

**Table 1.** The metabolomic studies and techniques applied to identify the mechanisms of abiotic stress tolerance in the Solanaceae family members

Sl. No	Plants studied	Techniques used for the study	Type of Stress	Major metabolites analyzed	Key findings	Citations
1.	Potato ( <i>S.tuberosum</i> and <i>S.acuale</i> )	GC-MS	Freezing tolerance	metabolites except ABA and SA	Types of aminoacids, sugars and other metabolites were reported to be different in chilling stress-treated samples. SA and ABA signalling pathways were activated in response to chilling stress treatment. <i>S. acuale</i> reported to be more freezing tolerant than <i>S. tuberosum</i> .	(17)
2.	Habanero ( <i>Capsicum chinense</i> )	LC-MS	Salinity, nitrogen and phosphorus deficiency	Edaphic stress	The work was for untargeted metabolomics, measuring changes in the Habanero fruit pericarp under increased salinity and nitrogen and phosphorus deficiency at three ripening stages. The result shows a metabolite substitution under nitrogen deficiency in the pericarp. Phosphorus deficiency showed an overall decrease in metabolite diversity and a negative impact on postharvest shelf life.	(18)
3.	Bell pepper	GC/Spectrophotometry	multiple stress interactions (SA and H <sub>2</sub> O <sub>2</sub> )	Phenolic compounds, low molecular weight metabolites campesterol, stigmasterol, (-tocopherol, succinic acid, asparagine and ascorbic acid. In addition to glyceric, fumaric, maleic acid and isoleucine	The study was conducted to analyze the effect of multiple stress interactions, elicitor concentrations and electrical conductivity on the concentration of secondary metabolites to relate their response to metabolic pathways. Shows significant change in aminoacyl t-RNA and valine-leucine-isoleucine biosynthesis and alanine-aspartate-glutamate metabolism, glyoxylate-dicarboxylate cycle, arginine-proline and citrate.	(19)
4.	<i>Withania</i>	LC-MS	Salinity	glycyl-hydroxyproline (8X), tyrosyl-valine (2X), 3-hydroxy-beta-ionone	The investigation was on the effect of NaCl on growth, photosynthesis, biochemical traits, tissue-specific withanolide and untargeted metabolites in <i>W. somnifera</i> . NaCl stress significantly enhanced withaferin A, withanolide A and withanone. LC-MS-based untargeted metabolite profiling revealed 37 differentially accumulated metabolites, including glycyl-hydroxyproline (8X), followed by tyrosyl-valine and 3-hydroxy-beta-ionone.	(20)
5.	Potato	UHPLC-HRMS/MS; LC-MS and NMR; Q-Exactive high-resolution tandem mass spectrometer equipped with heated ESI	post-harvest stresses such as wounding and light exposure	Steroidal glycoalkaloids (SGA)	Two-year research conducted on Magnum Bonum and five other table potato cultivars has been reported for their SGA content under light exposure. The result of the study shows that Magnum Bonum has a high SGA response to light exposure and the variety Binije has a decrease in SGA content under the same treatment. The study results also reveal the separate metabolic regulation pathways of SGA and calystegine levels in situations of increased accumulation of SGA.	(21)
6.	<i>Capsicum annuum</i> L	LC/MS/MS	Cold stress	Polyamene, hormone, osmolyte, putrescine, spermine, spermidine, ABA, JA, raffinose and proline	Two Capsicum cultivars (cold-sensitive, XS and cold-resistant GZ) were analysed in this study to analyse the response to cold stress. Metabolomic profiling shows that the content of metabolites like PAS, plant hormones, osmolytes, putrescine, spermine, spermidine, ABA, JA, raffinose and proline is increased under cold stress. The study also reveals that there is a deviation in MAPK signalling and (ROS) signalling pathways in response to cold stress in <i>Capsicum</i> .	(22)

7.	Pepper	LC-HRMS; UHPLC-MS	Cadmium (Cd) stress	Amino acids; fatty acid pathway; Volatile oil Compounds	<p>The study reports the impact of Cd-contaminated soil stress and nano-Selenium on the metabolism, fruit nutritional quality and volatile organic compound content in chilli pepper plants.</p> <p>Study includes the analysis of differential metabolites in roots and fruits, including amino acid metabolic pathways and capsaicin production pathways.</p> <p>Results show that the amino acid content (Pro, Trp, Argand Gln) in roots and fruits (Phe, Glu, Pro, Arg, Trp and Gln) is increased drastically by metallic stress.</p> <p>Volatile organic compounds like amyl alcohol, linalool oxide, E-2-heptadehyde, 2-hexenal, ethyl crotonate and 2-butanone, capsaicin, norhydrocapsaicin and dihydrocapsaicin levels also were seen to increase under metallic stress.</p>	(23)
8.	Potato	<sup>1</sup> H-NMR; LC-MS	Polluted water, [Fly Ash (FA) treated Acid mine drainage (AMD)]	secondary metabolites	<p>Reports of the study revealed the usage of analytical platforms like 1HNMR and LC-MS to identify the metabolites in potato plants which are treated with different concentrations of FA and AMD.</p> <p>The results of the analysis revealed the change in both primary and secondary metabolites. A significant increase in the production of secondary metabolites was noted in plants irrigated with 75 % FA: AMD concentration in the mixture .</p>	(24)
9.	Capsicum	UPLC-QToF MS	Cold and salinity	flavonoids	<p>In this study two <i>Capsicum</i> species were exposed to chilling, salinity stress and its combination to investigate the impact of these stresses on metabolome content in leaves. Study results show that chilling stress increases secondary metabolism and salinity stress decreases cell wall modification and solute transport.</p> <p>Metabolome profiling shows enhanced production of flavonoids like apigenin, rutin, kaempferol, luteolin and quercetin in <i>Capsicum</i> biomass residues in response to chilling or salinity stress or their combination.</p>	(25)
10.	<i>Capsicum annuum</i> L.	UHPLC-QE orbitrap/MS analysis; LC-MS/MS analyses	Cold stress	Polyamenes, phytohormones, osmolytes	<p>In this study, pepper lines with different levels of storage resistance, A 144 and A 361, are used for physiological examination, transcriptomics and metabolomics on different days of post-harvest.</p> <p>The study shows the genes responsible for ethylene-responsive transcriptional factor (ERFs), polygalacturonase (PG), cellulose synthase (CESA), abscisic acid insensitive (ABI) &lt; protein kinase 2 (SnRK2), and protein phosphatase 2C (PP2C) and metabolites such as phenylalanine and glycyltyrosine are expressed differently in various storage times.</p> <p>The study shows the variation in flavonoid biosynthesis, GSH metabolism and cysteine and methionine metabolism pathways.</p>	(22)
11.	<i>Capsicum annuum</i> L	HPLC-MS/MS	Storage	Phenylalanine, glycyl-tyrosine	<p>The study reports about the transcriptomics and metabolomics analysis of potato tissue samples under heat stress.</p> <p>Study results the variation (both upregulation and downregulation) of genes and variation in the production of compounds (both positive and negative) in leaf tissues in response to heat stress.</p> <p>Both metabolite and transcript enrichment for flavones and flavonol under prolonged heat stress were also noticed in this study,</p> <p>Study generates a novel set of metabolome and transcriptome profiles of potato under heat stress.</p>	(26)
12.	<i>Solanum tuberosum</i> L	LC-MS; UHPLC	Heat stress	Phenolics, Amino acids, Fatty acids, Steroids, Tyrosine, GSH, Isoquinoline alkaloids	<p>The study reports about the transcriptomics and metabolomics analysis of potato tissue samples under heat stress.</p> <p>Study results the variation (both upregulation and downregulation) of genes and variation in the production of compounds (both positive and negative) in leaf tissues in response to heat stress.</p> <p>Both metabolite and transcript enrichment for flavones and flavonol under prolonged heat stress were also noticed in this study,</p> <p>Study generates a novel set of metabolome and transcriptome profiles of potato under heat stress.</p>	(27)

13. Tomato LC-FTICR-MS and MS/MS Nitrogen deficiency, Chilling temperatures, Elevated light intensities Secondary metabolites (28)  
 This report is about a comparative analysis of the response of wild and cultivated varieties of tomatoes under diverse stress conditions, such as nitrogen deficiency, chilling or warm temperature, high light intensity and a combination of all. Observations of these experiments show that Nitrogen deficiency made a serious impact on the plants and induced secondary metabolism in both species. Cultivated variety had enhanced production of mono caffeoylquinic acids in response to nitrogen deficiency.
14. Tomato, eggplant and pepper LC-MS Comparative analysis of fruit metabolomics Fruit Polyphenolics (29)  
 The work reports about a comparative study on fruit metabolomics to elucidate the metabolic regulation of fruit polyphenolics in major Solanaceous crops viz, tomato, eggplant and pepper. Comparison among various cultivars of pepper (*Capsicum annuum* cv.) cultivars also were conducted. LC-MS based metabolomic analysis showed metabolic shift between hydroxycinnamates and flavonoids in *Capsicum* and anthocyanin in *Capsicum* cultivars.
15. Tobacco UHPLC-Q-TOF/MS Effect of coronatine in polyethylene glycol (PEG) stress Sugar, Sugar derivatives, organic acids, nitrogen-containing compounds (30)  
 The effect of coronatine in tobacco under polyethylene glycol (PEG) stress was analysed. It is noticed that the coronatine treatment ameliorates the polyethylene glycol (PEG) stress. Under osmotic condition enhanced metabolomic changes were noticed in tobacco leaves. The study shows that the essential metabolites, such as sugars, sugar derivatives, organic acids and nitrogen-containing compounds, play a crucial role in osmotic stress management in tobacco plants.
16. *Capsicum annuum* L. database MWDB; Partial least squares-discriminant analysis (PLS-DA) Heat Stress Sugars, Proline, Total protein, (31)  
 In this study a comparative analysis were conducted between heat sensitive and heat-tolerant cultivars (17CL30 and 05S180) Study showed accumulation of a huge number of diverse metabolites in both sensitive and tolerant cultivars under study The results reveal that the GSH metabolic pathway plays a crucial role in *Capsicum* in response to heat shock.
17. Potato GC-MS Stress to phosphate-based fungicide Sugar and alcohol (32)  
 The impact of phosphate-based fungicide on potato tubers was studied by the application of the fungicide through foliar and post-harvest application. GC-MS based studies showed that metabolites like sugars, amino acids or alcohols are accumulating in response to stress.
18. *Withania* GC/MS Drought stress Isoprenoids, phenols and alkaloids (33)  
 Water stress had induced in *Withania somnifera* and the drought stress tolerance related metabolic data were observed in this study. It is noticed that the biosynthesis of minor compounds like isoprenoids, phenols and alkaloids is increased under water stress. Pathways leading to glucose, fructose, fructan production and interconversion of triose phosphates to hexoses and hexose phosphorylation were noticed to be increased under water stress.

19.	African Egg plant	GC-MS/MS	Drought stress	Amino acids, sugars and organic acids	GC-MS studies were reported in 19 accessions of African eggplants under drought stress during different growth stages. Proline, glutamate, sucrose, fructose and tricarboxylic acid cycle metabolites were shown to accumulate in response to stress.	(34)
20.	Tomato	LC-QTOF-MS	Heat Stress	Alkaloids, Polyamenes, Flavonoids	LC-MS-based studies of pollen metabolite of tomato plants were conducted during various developmental stages and under various range of heat stress It is observed that the heat stress causes accumulation of flavones in pollen grains Young pollen grains showed an increased amount of PAS and alkaloids, while in mature pollens, flavonoid content was higher.	(35)
21.	<i>Nicotiana benthamiana</i>	GC-MS	Water stress	Sugars, Sugar alcohols, Amino acids	GC-MS studies were conducted in <i>N. benthamiana</i> plants to analyse metabolomic responses under fungal infection. From the leaves of infected plants, sugars, Amino acids, fatty acids and sugar alcohols were detected. Fungal-infected plants under water-deficient conditions show enhanced production of metabolites like cytosine, diethylene glycol, galactinol, glycerol, heptadecanoate, mannose, oleic acid, proline, rhamnose, succinate and urea. Fungal colonisation also showed an increase in root dry mass and relative water content under drought stress. All over the research results indicate that the fungal colonization enables the plant to defend against water stress more effectively.	(36)
22.	Tomato	LC/MS; LC/MS2; GC/MS	Drought stress	Amino acids, Carbohydrates, Cofactors, Prosthetic groups, Secondary metabolites and Xenobiotics	Deviations in metabolites, physiology, m RNA levels and promoter dynamics under drought stress in tobacco plants were analysed in this study Both general (the responses common in most plants) Species or family-specific responses to drought stress stimulations were observed in this research. Tobacco/Solanaceae specific metabolite 4-hydroxy-2-oxoglutaric acid (KHG) content in roots shows abundance under water deficit stress. In this study serine and glycine content reported to be decreased in leaves and roots under drought stress. Higher rate of accumulation of compatible solutes (sugars, alcohols, oligosaccharides, oxidative products of ROS amelioration).	(37)
23.	<i>Nicotiana langsdorffii</i>	HPLC coupled to High resolution mass spectrometry (HRMS)	High Temperature, Water deficit, high chromium (Cr) concentrations,	Lipids, acylsugars and glykoalkaloids, PAS	The response of the wild and transgenic <i>Nicotiana</i> species to diverse abiotic stresses, viz. high temperature, water deficit and high Cr concentrations, was analyzed. Impact of introduced genes under abiotic stresses were studied using HPLC coupled to HRMS. It was noticed that heat stress induced a set of special metabolites. Enhanced production of acylsugars and glykoalkaloids also were reported. Combination of drought and Cr Stress showed increased antioxidant levels and repaired lipids.	(38)

24. Tomato LC-MS and GC-MS Nitrogen, Phosphorus and Potassium-deficient soluble sugars; amino acids; soluble sugars and amino acids  
 Difference in content of metabolite components like amino acids, organic acids and soluble sugars in xylem sap of Tomato plants under macro nutrients (N, P, K) deficient conditions were studied using liquid chromatography in this research. (39)  
 The nutrient deficiency is reported to increase the metabolite concentration in xylem sap. Increased concentration of  $\gamma$ -aminobutyric acid (GABA) and glutamine was reported in the xylem sap content under nutrient scarcity, in addition to organic acids and soluble sugars.
25. Tomato GC-MS/MS low oxygen stress Glycolysis and TCA cycle products  
 The study aimed to analyse the metabolic responses of plant organs to low oxygen, in cultured tomato cells. (40)  
 The study shows the increased intermediates of glycolysis in addition to increases in lactate and sugar alcohol content under low oxygen stress. Enhanced fermentative metabolism and sugar alcohol synthesis while hindering the TCA cycle also were noted in the studied samples.
26. Tobacco HPLC-MS/MS Water stress Phenolic compounds  
 Variation in phenylpropanoid profile in *Nicotiana tabacum* L.c. Two different conditions, i.e., senescent and non-senescent parts of the plant and watered or young plants with water deficit, were analysed. (41)  
 It is reported that there is an increase in concentration of polyphenol compounds under water deficit or senescence. But the concentration of 3-Hydroxycinnamic acid amides (HCAA) was less in senescent samples. 5-O-caffeoylquinic acid (neochlorogenic acid) was reported in all the samples. This study reported the presence of kaempferol-7-O-neohesperidoside for the first time from *Nicotiana tabacum* samples.
27. Tomato cultivars HPLC/UV-PAD/ESI-MSn Water stress Phenolic metabolite  
 Drought tolerance capacity of five different cherry tomatoes was studied in this research. Decrease in shikimate pathways and phenolic compounds under water stress were reported in this study. (42)  
 The cultivar Zarina showed more tolerance to water stress with enhanced activities of flavonoid and phenylpropanoid production and reduction in degradation-related enzymes.
28. Tomato GC-MS Water stress TCA products  
 Fruit samples from the irrigated and non-irrigated tomato plants (cultivars and hybrid varieties) were analyzed using GC-MS-based metabolite profiling. Significant deviation in amino acid concentrations was shown in both varieties and cultivars under study. (43)  
 Increase in concentration of fatty acids and organic acids were reported in hybrid variety under water stress. Variations in sugars, sugar phosphates, sugar alcohols and many other metabolites were observed in both the genotypes under investigation. Increase in amino acid contents, alanine, aspartate, GABA, glutamate, glycine, homoserine, isoleucine, proline, serine and valine were reported, but a decline in cysteine, glutamine and glycine was also observed in this study.

chemical modification of the molecules and the sample is prepared in liquid form. With advances in technique, different types of columns are available which include stationary phase with different size and chemical properties. The selection of columns comprised of ion exchange, reverse phase, hydrophobic interaction column (16). For high resolution and sensitivity, Ultra-Performance liquid chromatography (UP-LC) is used (48). An atmospheric pressure ionisation (API) interface is used to connect LC with MS. The API technique comprises atmospheric pressure chemical ionisation and electrospray ionisation (16). These techniques are soft ionisation techniques and do not break the macromolecule. There are many MS instruments, including magnetic analysers, quadrupole and TOF spectrometers. Two MS can be used in combination such as Q-TOF mass analyser (16). Various built-in software tools are available for LC-MS analysis. Liquid chromatography mass spectrometry is a better technique than GC-MS for the analysis of thermostable compounds. A common problem in LC-MS includes the pressure shock, which affects column efficiency. Table 1 lists metabolomic research and methods for identifying abiotic stress tolerance mechanisms in members of the Solanaceae through a variety of liquid chromatographic techniques.

An LC-MS-based metabolome database (MoToDB) for tomato is available for covering metabolomics of its fruits (49). High-performance liquid chromatography analysis of samples from the vegetative parts of salinity-stress-induced *Solanum incanum* plants shows variation in glycoalkaloid content, including Solamargine and Solasonine (50). Researchers reported the LC-MS-based quantification of SGAs from *Solanum xanthocarpum* (51). Another study reports the use of reversed-phase high-performance liquid chromatography coupled with diode-array detection to detect steroidal glycosides across different *Solanum* species (52). Liquid Chromatography Mass Spectrometry-based identification of phytochemicals, viz. Solasonine, Solamargine and other triterpenoids from *Solanum nigrum* L. are reported by scientists (53). High Performance Liquid Chromatography and LC-MS studies have been reported on sodium chloride (NaCl) induced salinity stress and its impact on secondary metabolite content in *Solanum villosum* Mill. The results of the study show a considerable increase in leaf contents of Caffeic acid, Lutein and beta-carotene in *S. villosum* under NaCl stress (54). High performance liquid chromatographic studies show that exogenous application of Abscisic acid (ABA) increases the synthesis of phenolic compounds in *Physalis angulata* L. (55). A comprehensive glycoalkaloid profiling from the vegetative parts of underutilised Solanaceae plants was reported using HPLC-TOF-MS. The study presents a profile of 51 GAs at varying concentrations across different species (56).

Reports on phytochemical studies of genetically modified and wild varieties of *Nicotiana* species (*N. glauca* and *N. langdorffii*) using High-performance liquid chromatography-tandem mass spectrometry (HPLC-MS/MS) and GC-MS provide a better understanding of phytohormones (57). Ultra-high-performance liquid chromatography-mass spectrometry (UHPLC/MS) was reported to be used effectively for profiling acyl sugar diversity in various species of *Solanum* (*S. lycopersicum* and *S. habrochaites*).

#### **Nuclear magnetic resonance spectroscopy**

Nuclear Magnetic Resonance (NMR) spectroscopy is a physical process in which atoms with non-zero magnetic moment get

flipped under the influence of a magnetic field and electromagnetic radiation (16). Atoms with nonzero spin and nonzero net magnetic moment are  $^1\text{H}$ ,  $^{13}\text{C}$  and  $^{31}\text{P}$ . In the case of  $^1\text{H}$  NMR, the H atom aligns with the direction of the applied magnetic field and is flipped when electromagnetic radiation of a specific frequency is applied; this flipping is known as resonance. When this flipping occurs, the signal is generated. The neighboring environment and the electron cloud around the H atom shield or de-shield the atom, thereby affecting the signal position and chemical shift. Neighboring H atoms also influence one another, causing signal splitting. When analysing a mixture, 2D NMR is advisable. 2D NMR includes Correlation spectroscopy (COSY), Heteronuclear single quantum coherence (HSQC) and Heteronuclear multiple bond coherence (HMBC) (58). Nuclear magnetic resonance is less sensitive than MS but remains a powerful tool for identifying and quantifying metabolites in plants (59). Because NMR is nondestructive, spectra from cell suspensions, tissues and even entire plants can be recorded (48).  $^{31}\text{P}$  is used to profile phosphate esters and  $^{13}\text{C}$  is used to profile amino acids, lipids etc (60). Reports are available on the successful application of NMR techniques for metabolome profiling of members of the Solanaceae under abiotic stress (61–63).

#### **Effect of drought stress on the metabolome of Solanaceae family**

Drought stress causes significant morphological and physiological changes in plants, as well as other responses. Plants respond differently to water stress depending on the phenological stage at which it occurs, its duration and its severity (64). However, persistent high-intensity drought stress may impede plant growth, alter morphological traits and biomass distribution patterns, or even cause plant mortality (65). On a global scale, drought is undoubtedly the most challenging and harmful abiotic stress. According to one definition, a plant's ability to continue growing productively despite low leaf water status is its relative drought tolerance. Due to solute concentration gradients and osmosis, drought reduces the cell's water potential and causes it to lose turgidity. Some plants can modify their osmotic potential to endure dehydration or maintain turgor pressure by actively accumulating solutes known as osmo-protectants or compatible solutes. Plants have developed a variety of defense avoidance and tolerance methods to deal with drought stress (66). Additionally, plants under drought stress assemble more reactive oxygen species (ROS), such as hydrogen peroxide ( $\text{H}_2\text{O}_2$ ) and the superoxide anion ( $\text{O}_2^\bullet$ ) (67). Secondary metabolites in plants are crucial to how they respond to stress (68). Drought exposure results in a sharp drop in physiological and plant growth indicators. Through antioxidant defense mechanisms, plants can tolerate damage caused by oxidative stress (69, 70). Furthermore, under stress, plants can maintain osmotic balance and quickly repair oxidative damage due to the accumulation of osmolytes such as proline and carbohydrates (71, 72). Another common response of plants to stress is changes in the expression levels of phytohormones (73). There were reductions in the potato plant's shoot and root length, shoot and root dry weight and leaf area. It was shown that drought stress decreased total chlorophyll a and b concentrations in potato. Stress from the drought decreased the expression of the examined hormones, including indole acetic acid, Indole-3-butyric acid, GA1 and GA4, in potato plant tissue (74). In tomato, leaf stomatal conductance is strongly impacted by drought stress. In drought-stressed plants, the photosynthetic

efficiency was also reduced (75). Strigolactones aid shoots in adapting to drought, as strigolactone-depleted plants are susceptible to drought due to stomatal hyposensitivity to ABA. In contrast, roots' reduced synthesis of strigolactones during drought suggests that their digestion and function are organ-specific. Since strigolactones may be transmitted acropetally, such a decline may also affect shoots as a sign of systemic stress throughout the body (76). Drought downregulates cyclin-dependent kinase activity, reducing the number of meristematic cells and slowing cellular division and extension, which results in fewer leaves and less leaf area (77–80). Under drought stress, the plant produces fewer fruits overall and fewer fruits per unit area and under water stress, it produces fewer fruits overall. There are reports about lower concentrations of micronutrients, viz. N, K, zinc (Zn) and manganese (Mn), in plants cultivated in water-restricted environments, except for P (64). Fruits with a bitter taste may result from dry conditions and extreme heat (81). Long-term drought stress reduces bloom production and causes early blossom fading.

A greenhouse experimental study on the interaction of drought-stressed potato plants with entomopathogenic nematodes (EPNs) reports that the drought stress weakens the tritrophic interaction (82). Detailed investigation of the effect of water deficit on the growth and development of various Solanaceae was reported by various researchers (83). A study on phenotypic and physiological variations in tomato leaves under dehydration treatment reported that severe damage occurred after 24 hr of treatment and, as with drought stress, dehydration increased ROS accumulation. Transcriptomic analysis of the treated samples shows a significant number of DEGs including Transcription Factors (TFs) of various families and drought-responsive genes. The study verified the expression pattern of various TFs (84).

In a study, the variations in metabolomic pathways in tomato seedlings in response to developmental and environmental cues were analysed. The study reveals the interplay between depletion of stored molecules and de novo synthesis. Results of this study give information on metabolic networks regulating flavonoid biosynthesis in tomato (85). Based on the report of a comparative metabolomics study of two hybrid varieties of tomato, the hybrid HTT VRNTH18283 performs better than HTS VRNTH19072 against the detrimental effects of high temperature due to its changed physicochemical profile, enhanced metabolite compositional diversity and discriminatory metabolite biomarkers.

Plants under drought stress produce compounds such as amino acids, which increase the concentration of soluble solids in fruits (86). During drought stress, mannitol, ononitol, myo-inositol, fructans, trehalose, proline, glycine betaine and polyamines (PAS) accumulate to considerable levels. It is reported that the production of tropane alkaloids, GAs and nicotine is enhanced by exposure to abiotic conditions. There is evidence that alkaloids such as atropine and scopolamine influence physiological responses to abiotic stress. In *Datura* high salinity is reported to be cause, high salinity has been reported to cause the accumulation of atropine. Similarly, nicotine content is also noted to be increased because of the influence of various environmental cues. Abiotic stress conditions like light exposure, mechanical injury and improper storage conditions have been shown to enhance the accretion of SGAs, Solanine and Tomatine in potatoes and tomatoes, respectively.

Additionally, certain proteins, including those encoded by genes for late embryogenesis abundant proteins and stress-sensitive transcription factor genes, are stored in plant cells as a stress-defense strategy (87). The roots and stems' weight while under drought stress decreased both wet and dry. It also decreased the relative water content (88). One of the plants' biological functions most susceptible to dryness is canopy development, which is driven by the irreversible elongation of individual plant cells (89). It harms essential molecules, including proteins, lipids and DNA (90). Drought stress further impairs product quality, such as by elevating common scab incidence, while disrupting multiple metabolic pathways that govern physiological and developmental processes (91, 92). Reduced ribulose biphosphate synthesis, reduced Rubisco activity and reduced carboxylation efficiency are examples of biochemical alterations. Under stress, the steady loss of maximal metabolic capacity saturates the photosynthetic rate, suggesting that ribulose biphosphate carboxylase/oxygenase and other enzymes of the photosynthetic emission reduction cycle are implicated. Restriction of ATP production likely limits ribulose biphosphate synthesis, driven by the coupling factor's gradual loss or inactivation due to rising ionic magnesium ( $Mg^{2+}$ ) concentrations. Photosynthesis under stress may be partially improved by selectively increasing the activity of Rubisco activase, a nuclear-encoded chloroplast protein, although such improvement is typically minimal (93). Reduced  $CO_2$  assimilation results in less  $NADP^+$  regeneration at the level of electron transport. Distinct signaling pathways activate appropriate transcription factors and initiate phosphorylation cascades that, in turn, mediate cellular responses to drought in potato. As the potato plant's main defense mechanism against stress, these transcription factors control gene expression. Complementary solutes help stabilise enzymes, preventing denaturation caused by drought stress. Potato plants' sophisticated adaptive modifications in response to limited water supply are frequently accompanied by negative pleiotropic impacts. As water stress increases, non-stomatal leaf components known as "mesophyll" significantly reduce transpiration (94). These effects lead to a global decrease in production.

### Effect of waterlogging on the metabolome of the Solanaceae family

Water logging stress is one of the main abiotic restrictions on growth, development, species dispersal and agricultural output. In plants stress is caused by deeper submersion and waterlogging of the soil. This stress is brought on by decreased oxygen availability for plant cells as a result of flooding or compacted soil. Floodwater blocks airflow by filling soil pores and because dissolved oxygen diffuses slowly in stagnant water, only a thin surface layer of soil contains oxygen. Crop losses from prolonged floods can reach > 10 % and in extreme circumstances > 40 %. The physiological functioning is disrupted, adversely affecting vegetative and reproductive growth. Stomatal closure, which impacts both gas exchange and passive water absorption while also severely affecting anaerobic conditions in the rhizosphere, is the earliest sign of flooding damage. Reduced transpiration causes early senescence and leaf withering, which ultimately leads to foliar abscission (95). Impaired morphological (reduced leaf area, early abscission) and physiological (lower photosynthetic efficiency in younger leaves, photoinhibition, affected PS II functionality) characters were reported in flooded plants of eggplants (96). A

comparative study conducted to assess the response of water stress (drought and flooding) in various genotypes of brinjal (*Solanum melongena* L.) and *Solanum microcarpon* L. reports the greater sensitivity of stomata under flooding than to drought in various *S. melongena* genotypes. The study also reports that some genotypes exhibit better photosynthetic performance under drought than under flooding. Variation in the speed of the stomatal mechanism also was reported from this study in response to extremes of water level (97). Various studies are available with reports on variation in morphological, biochemical and physiological parameters of solanaceous members under waterlogged conditions (98–103).

Root respiration shifts from aerobic to anaerobic conditions under flooded conditions, which are either inadequately (hypoxia) or completely (anoxia) non-aerated, in which gas transport is highly restricted. This is highly detrimental to plant growth. The availability of nutrients to plants is significantly reduced in soils with low  $O_2$  partial pressures. Anaerobic bacteria predominate when oxygen availability in the soil is limited, resulting in severely reduced conditions in the rhizosphere, where toxic concentrations of iron and manganese ions, hydrogen sulfide, sulfides, butyric acid and lactic acid accumulate (104). In the case of tomatoes, waterlogging increased *in vivo*  $H_2O_2$  levels, lipid peroxidation and relative ion leakage while decreasing chlorophyll content (105). In tomato, Na concentrations rose during waterlogging, whereas K concentrations fell. Decrease in the Ca level reported in roots of tomato as well as fat, protein and total solids dissolved all decreased, while fruit moisture, Phosphorus (P) and Sodium (Na) increased (106). In *Capsicum annuum* L., ROS are controlled, antioxidant activity increases, lignin is produced and stress-tolerance genes are expressed. Furthermore, waterlogging causes the accumulation of hazardous chemicals, including ethanol and ethanol produced by anaerobic respiration. Moreover, waterlogging increased alcohol dehydrogenase (ADH) activity, activated ABA sensors, activated ABA-dependent transcription and reduced ABA levels in pepper. Waterlogging can make it more difficult to synthesize ethylene. The direct precursor of ethylene, 1-aminocyclopropane-1-carboxylic acid, is produced in the anaerobic root and transported to the shoot, where it is promptly converted to ethylene, as previously reported (107). Waterlogging reduced leaf area and nitrogen use efficiency in tamarillo plants. Waterlogging episodes improved dry matter partitioning to stems (by about 30–35 %) (102). Eggplants are particularly susceptible to waterlogging during the blooming and fruiting stages (108). When it comes to tobacco, the amount of malondialdehyde (MDA) grew dramatically as waterlogging progressed, while the levels of chlorophylls and soluble protein declined. Superoxide dismutase (SOD), peroxidase and catalase (CAT) activities also differed in this direction, increasing initially before declining (103). The main ROS that harm proteins, lipid membranes and DNA include  $H_2O_2$ , hydroxyl radicals ( $\cdot OH$ ), ( $O_2$ ) and singlet oxygen ( $^1O_2$ ). In addition to impairing cellular function, lipid peroxidation of organelles and cell membrane enzymes cause membrane leakage and autolysis (109). Research is conducted worldwide to improve the plant's efficiency in responding to environmental cues and increasing production.

#### Effect of salt stress on the metabolome of Solanaceae family

Today, salinity is a significant global problem that affects agricultural productivity. High salinity affects approximately 33 % of irrigated agricultural lands globally and these regions are increasing by 10 % per year (110). Ionic and osmotic stresses are

the two major threats of salinity (111). Regions with naturally saline soil, irrigation with saline water, or seawater infiltration can cause soil that supports plant growth in coastal locations to become saline (112). Salinity is becoming a serious threat because of global warming. The sensitivity of plants to salinity varies greatly across growth stages (113). The stages that are most negatively impacted by salinity are seed germination and the seedling stage. Plant metabolism is greatly affected by salinity due to the ionic imbalance (114). When the soil's salt concentration rises and the water potential falls, the plant cell's pressure potential declines and the cell eventually stop dividing and elongating (115). Salt stress has a negative effect on multiple physicochemical processes in plants, such as photosynthesis, transpiration, etc. and it also affects the growth of vegetative and reproductive organs (116). Reactive oxygen species also increases in plants in response to salinity (117). With increasing soil salinity, germination percentage, germination time, dry weight and root shoot ratio of pepper, tomato, eggplant and seed and seedling of other glycophytic plants are severely affected (88, 89, 118–120). It alters plant ion concentrations and ultimately leads to the formation of ROS. Sodium ion ( $Na^+$ ) influx causes the efflux of the potassium ion ( $K^+$ ), which leads to the disturbance in the concentration of  $Ca^{2+}$  ion in capsicum (121). Potato salinity alters  $Mg^{2+}$  ion concentration in leaves, leading to stomatal closure. Sodium and chloride (Cl) ions reduce chlorophyll content (122). Sodium, calcium (Ca), K and Mg uptake in plant tissues under salinity stress is genotype-dependent (116). There is a notable reduction in the concentration of K, Ca and Mg ions with increases in salt concentration in pepper (109). In case of tomatoes, the administration of  $Ca^{2+}$  ions somewhat mitigates the effects of salinity (123). In potato, K<sup>+</sup> concentration in leaves declined with increasing salt levels, whereas it increased in stems and tubers (124). Proline is the primary osmolyte that accumulates when plants experience salt stress and it helps provide tolerance. Amount of proline accumulation differs across genotype, developmental stage and organs of plant. Proline also serves as an antioxidant, a stabiliser of subcellular structures, a regulator of cell redox homeostasis, a source of energy and a signaling molecule (125). In potato plant highest accumulation of proline is in stem tissue (126). The concentration of soluble protein in potato leaves drastically decreased in salt stress (127). Tobacco varieties subjected to salt stress showed a rise in the total amount of protein in comparison to the leaves of plants under control (128). Polyamines are also important molecules that play protective, regulatory and ROS-scavenging roles (129). Level of putrescine, spermidine and spermine increased significantly under salinity stress in tomato cultivars (93). To counteract the oxidative stress plant has antioxidant system which includes both enzymatic and non-enzymatic antioxidants. Some of the major enzymatic antioxidants are SOD, POD, CAT and Glutathione Reductase (GR). Some non-enzymatic antioxidants include flavonoids, carotenoids, vitamin C and vitamin D. Levels of antioxidants in plants are genotype- and organ-dependent. Malondialdehyde and  $H_2O_2$  are indicators of oxidative stress. As the concentration of salt increases, the levels of MDA and  $H_2O_2$  also increase in tomato (130) and similar results were observed in potato (131) and capsicum (90). In huckleberry there is no significant change in MDA content but in eggplant it increased markedly (91). Plants with higher levels of antioxidants show greater tolerance to salinity than plants with lower levels of antioxidants in the cell. Salt-resistant varieties showed increased overall phenolic levels (132). In

eggplant leaves, CAT activity increases, whereas in roots it decreases. Glutathione reductase activity increases in huckleberry roots, whereas in leaves there is no significant change (91). In some potato cultivars, SOD activity increases and CAT activity decreases (133). High concentration of salt boosts up activity of ROS-scavenging enzymes like CAT, Ascorbate Peroxidase (APX) and GR in salt-tolerant potato cultivars (99). Salinity has a significant effect on the amount and nutritional value of the fruit, delaying flowering and fruit ripening. In pepper fruit, the number and size decrease, whereas the capsaicinoid content increases and Vitamin B<sub>6</sub>, Vitamin B<sub>12</sub> and Vitamin C decreased (86). In tomato fruits, osmotic and water potentials were reduced and the fruit cuticle's water permeability decreased (134). With the growing population it becomes necessary to make stress tolerant varieties to fulfill the needs of the world. Red pepper becomes tolerant when proline and L-tryptophan are applied exogenously in combination (89). N-supplementation lessens the detrimental effects of salt on agricultural production (135). Application of Se on the leaves can increase the tolerance in eggplant against salt stress (136). Salicylic acid and GSH play significant roles in conferring salinity tolerance in tomato (93, 137).

### Effect of temperature stress on the metabolome of the Solanaceae family

The most vital abiotic factor affecting all organisms' life processes is temperature. Temperature is a significant environmental variable that varies with the seasons and undergoes periodic fluctuations. Consequently, plant cells must be able to detect changes in the surrounding temperature and convert this information into flexible physiological responses. The mechanisms governing intracellular temperature signaling are essential for regulating the emergence of resistance to heat or cold stress under severe temperature conditions (138). The three different forms of temperature stress that plants typically undergo are (a) chilling stress (occurs during below freezing temperature), (b) freezing stress (occurs during above freezing temperature) and (c) heat stress. This demonstrates how plants' physiological and metabolic processes are affected by both low and high temperatures and the effects of the plant's resistance to high and low temperatures or the potential for adaptability (139). Temperature, as well as other environmental factors (e.g., light, nutrients and moisture), has a significant impact on how tomato plants respond during the vegetative and reproductive phases. Various studies have shown the detrimental effect of environmental changes, such as high or low temperature stress on the tomato growth. The rates of various biological processes are influenced by temperature, which is also a critical factor in tomato fruit development (140). Tomato plants can also withstand a broad range of temperatures; it has long been known that high daytime temperatures negatively affect fruit yield when temperatures exceed 32 °C, especially when nighttime temperatures exceed 21 °C. For the tomato, extreme temperature stress at 30 °C and 45 °C has been shown to significantly reduce anthesis, blossom drop and fruit set. Critical pre-anthesis high-temperature stress was associated with reduced pollen production, epidermal and endothelial abnormalities and other developmental alterations in the anther (141). The photosynthetic system is severely damaged by high-temperature stress (140). There are a number of manifestations that prevent tomato fruit from setting at high temperatures, including: underdeveloped flowers, bud drop, poor fertilization, style

elongation, slowdown of pollen tube growth, reduction in carbohydrate availability, sugar metabolism is slowed and viable pollen generation is ineffective, abortion of the ovule and endosperm deterioration. The influence of a rather low nighttime temperature of 13 °C for optimal tomato fruit set had already been noted long before and this phenomenon was known as thermoperiodism. Subsequently, research in the phytotron established that lowering nighttime temperature by 15–20 °C significantly increased the biological and commercial production of tomatoes (141). Tomato metabolism can be significantly altered by exposure to elevated temperatures. In tomato plants cultivated at high temperatures (35 °C), H<sub>2</sub>O<sub>2</sub> accumulates and cannot be removed by the GSH/ascorbate cycle, as the same high temperature may have rendered its primary enzymes inactive. This buildup of H<sub>2</sub>O<sub>2</sub> would initially decrease foliar biomass before killing the plant. On the other hand, tomato plants cultivated at the optimal temperature (25 °C) develop effectively, exhibiting efficient active oxygen species (AOS) detoxification and, consequently, proper functioning of the plant's antioxidant systems (142). During fruit development, isocitrate levels fluctuate during post-harvest storage. At high temperatures, pollen development becomes sensitive and pollen viability declines, a reduction linked to decreases in metabolites such as PAS and carbohydrates (36). During low temperature, sugars, phenolic substances accumulate i.e., flavonoid content increases, whereas other metabolites like SA, ABA and raffinose content also increase, amino acid content, i.e., leucine, isoleucine, valine, phenylalanine and alanine, decreases (143). Early planting conditions in the north-western plains and India are limited by the adoption of potatoes due to high temperatures during crop growth and tuberization. Potato quality and yield are highly sensitive to high temperatures (144). Potato has temperature needs i.e., the optimal and limit values for growth of the above-ground portion and for tubers are different. In potatoes, hilum growth occurs at a rate of 20 to 25 °C, whereas 15 to 20 °C is the optimal temperature for tuber growth and tuberisation. Reduction in the potato tuberisation and acceleration in the growth of plants above ground parts occur at temperatures greater than those considered appropriate (145). When the temperature is low, it favours tuberisation, which is reduced during nighttime temperatures over 20 °C and is completely inhibited at temperatures over 25 °C. The two main processes for dealing with abiotic stresses are melatonin-mediated ROS scavenging and activation of the antioxidant defense response. Furthermore, it functions as a key regulator of plant defense mechanisms in response to environmental stresses by regulating genes associated with pathogenesis, antioxidant enzymes and stress-specific genes (146). During daytime temperature enzymes like fumarate, citrate and fumarate decreases in tubers as well as in leaves. At high temperature, photosynthetic capacities of leaves are enhanced and there is a decrease in the tuber and leaf content of the amino acids (147). Even the starch accumulation and photosynthesis capacity decreases because of the loss of chlorophyll content and carbon transport inhibition. Several metabolites, i.e., amino acids like histidine, as well as N-containing compounds and hormones, include JA decreases (28). In temperate locations, sweet peppers are cultivated as an annual crop. The ideal temperature for sweet pepper growth is between 20 and 25 °C. Growth is typically slowed down and yield is reduced when temperature goes below 15°C or rises over 32°C (148). Warm temperatures (between 21 and 29 °C),

wet soil and moderate temperatures are ideal growing conditions for bell peppers. Low temperature is an environmental condition that significantly affects plant growth, including photosynthesis, water uptake and nutrient uptake. Crops with such economic importance as pepper, which influences the yield as well as the quality of such crops (149). During low temperature, SA significantly reduced MDA content and ( $O_2^{\bullet}$ ) production. Even before the onset of heat stress, SA treatment enhanced  $O_2$  scavenging, POD activity and GSH accumulation (150–153). High levels of metabolites, i.e., sugars, PAS and amino acids, i.e., proline, increase considerably during low temperature (154). On the other hand, plants' responses to high temperatures are significantly influenced by the intricate metabolic regulatory networks. High temperature reorganises the metabolic state to maintain homeostasis. For instance, the high temperature is influenced by proteins, free proline, glycinebetaine, soluble carbohydrates, phenolic substances and lipids. These metabolites also help plants produce metabolites in response to heat stress by maintaining osmotic balance and conferring HS tolerance. Main osmotic adjusting materials in plants i.e. amount of protein, proline and total soluble sugars are enhanced. Flavonoids act like antioxidants to eliminate the ROS produced by the HS, that play the essential role in treating the HS response. MDA content rises as well (32). The ideal temperature for *Nicotiana Tabacum* L. throughout its field growing phase is between 22 and 28 °C and during its mature stage, the temperature shouldn't drop 20 °C below because of its sensitivity to low temperatures. When temperature falls below 10 to 13 °C, tobacco plants are unable to grow and at 2 to 3 °C, plants will die (155). Numerous tightly controlled metabolic networks in plants can be crucial to their growth when exposed to the low temperature. It has been studied that the exposure to the cold triggers the expression and/or activation of numerous metabolic processes. Since they are necessary for essential proteins production and also form the wide range of metabolic products with numerous roles in the responses of plants. For e.g. amino acids are well as the sugars are recognized during low temperature. The content of amino acids i.e. serine, valine, tyrosine, leucine and L-aspartate increase in greater amount. Hormones such as gibberellin, ethylene, auxin and ABA are regulated during low temperature (156). Majority of tropical vegetables as well as fruits including the brinjal, are sensitive. Less than 10 °C, brinjal plant experience physiologic problems that are primarily shown by the development of external wounds like scalding and pitting, browning of the flesh as well as the seed darkening (157). The range of 22 to 28 °C is ideal for the growth and development of eggplant (158). During the cool season, when temperature stress is low in brinjal, the loss of pollen fertility occurs, as well as the parthenocarpic fruit formation, but the female fertility is not affected at all. Effect of the temperature on the male sterility is transient and normal seed development restores full pollen fertility as temperature conditions improve (159). During high temperature stress, it often causes an increase in the production of ROS like  $H_2O_2$ , ( $^1O_2$ ),  $\cdot OH$  as well as ( $O_2^{\bullet}$ ) all of which can cause the denaturation of the proteins, damage to the nucleic acid and the lipid peroxidation and nucleic acid damage in brinjal. To confront the ROS damage, plants have generated the enzymatic system and as well as Brassinosteroids are type of essential steroidal plant growth regulator that promote germination of seed, elongation of the cell and cell division in brinjal (160).

Studies report that young leaves and developing reproductive organs contain a range of biochemicals like organic and amino acids, nitrogen-containing compounds, lipids and secondary metabolites, which enable the plant for defense mechanisms (161).

In another study, a cross-cultivar comparison between various pepper cultivars (*Capsicum annuum* cv.) using LC-MS and a cross-species comparison of fruit-metabolomics to clarify the metabolic regulation of fruit polyphenolics from three representative crops of Solanaceae (tomato, eggplant and pepper), a metabolic trade-off between flavonoids and hydroxycinnamates in anthocyanin-type and spicy pepper cultivars and found fruit polyphenolic metabolic signatures in each species from various tissue types and fruit ripening stages (28).

In an experiment to elucidate the physiological and biochemical processes of tomato plants' leaves as well as their flower and fruit set throughout the reproductive stage under waterlogging stress in six genotypes of tomato it shows that height of plant, diameter of stem, number of inflorescences, weight of single fruit and per plant are significantly affected negatively under water logging in addition to chlorophyll content, low net photosynthetic rate, low diffusion of gas and impaired rate of transpiration and antioxidant system. The study also reports elevated MDA and  $H_2O_2$  levels across all screened genotypes under stress (162).

To identify eggplant cultivars that withstand waterlogging and are suitable for summer growth, a field experiment was conducted with 10 genotypes. It was found that the variety BARI Hybrid Begun-6 demonstrated superior performance compared to other varieties and lines and appears promising for the summer season (103).

### Integrated approaches

To address the issue comprehensively, an integrated research approach that combines multiple disciplines, methodologies and data sources is essential. There are numerous reports on integrated “omics” approaches to elucidate abiotic stress tolerance mechanisms in Solanaceae species.

An integrated “omics” approach (physiology, metabolites, mRNAs and promoters) to drought stress responses in tobacco and other common Solanaceae members (tomato and potato) revealed that many drought responses are family- and species-specific (163).

The pathogenesis-related protein 1 (PR-1) gene family is reported to play a crucial role in plant biotic and abiotic stress responses and metabolism. Scientists reported a study on the PR-1 gene family in *S. lycopersicum* L., which identified 13 novel S1PR-1 genes. Bioinformatics analysis (KEGG annotation) of this study showed that the S1PR-1 proteins worked in the environmental information processing (09130) (164).

A compilation report on genomics, proteomics and metabolomics research to enhance the abiotic stress tolerance of the tomato plant was published recently (165). RNA-seq studies of *S. melongena* and its wild relative (*S. dasyphyllum*) under various osmotic stress conditions revealed that *S. dasyphyllum* is an excellent genetic resource for breeding experiments for stress-tolerant eggplant varieties (87).

A group of researchers reported the tissue-specific modulation in gene expression of key genes and pathways associated with various proteins under high temperature stress in various parts of the sweet potato (leaf, tuberous roots, fibrous roots) (166). A comparative study to analyse the response of aerial and ground parts of *H. annuus* and *S. lycopersicum* in Na<sup>+</sup> and K<sup>+</sup> intake during salt stress (NaCl) reveals that in both the plants, the concentration of melatonin increases as in direct proportion to the intensity of salinity stress and Na<sup>+</sup> and K<sup>+</sup> are accumulated in roots and stem in *H. annuus* but in fruits and roots in *S. lycopersicum*. In this study the very low-level K<sup>+</sup> was reported in seeds of *H. annuus* and fruit and root of *S. lycopersicum* (142).

Genomic studies report the list of genes and gene families involved in the drought stress tolerance in Solanaceae members. Tissue-specific transcriptomic responses were reported from the leaves and roots of *Petunia* hybrid Mitchell under salt stress (167). Expression analysis study of tomato ammonium transporters 1 (SIAMT1) genes under osmotic stress (drought and salinity stress) was reported by researchers. The study shows variation in SIAMT1s at both the nucleotide and protein levels. The study concludes that the SIAM1-3 genes exhibited distinct expression patterns compared with others. This study further demonstrates that abiotic stress conditions negatively affect SIAMT1 expression (168).

Phenotypic analysis of trichomes in *Solanum* species, under field conditions, reveals increased trichome density and stomatal size under water-deficit conditions (169). In a study, HPLC coupled to high-resolution mass spectrometry (HRMS) allowed the identification of more than 200 metabolites in *Nicotiana langsdorffii* Weinm. under exposure to different abiotic stress conditions, viz., water deficit, high temperature and high chromatin concentration (170).

## Conclusion

With increasing population, demand has also risen; therefore, it is necessary to increase production to meet people's needs. But increasing global warming, low rainfall and soil degradation caused by excessive fertiliser use and other factors affect plant growth, reducing productivity and yield. The plant responds to different stresses by altering metabolite concentrations across tissues, thereby enhancing resistance. These metabolites help to counteract the stress condition. More than one lakh metabolites are present in plants which include both primary and secondary metabolites. But with the existing technology, we are able to identify only a few metabolites rest are still unknown to mankind. Advancements in technology and improvements to existing methods are needed to identify metabolites with greater precision. The phenotype of a plant can be predicted by integrating both genomics and metabolomics, which is helpful in crop breeding. Like proline and SA, many more chemical compounds can be identified that help plants withstand harsh stressful conditions. Since the Solanaceae family members are important and have nutraceutical values so their resistant varieties should be developed. With the help of metabolomics, it can be studied which development stage and which organ of the plant is more affected due to stress so farmers can take necessary actions to minimise the effect of stress.

There are several critical gaps in metabolomics research on Solanaceae that remain fragmented and incomplete, despite extensive research on physiological and transcriptomic studies in Solanaceae crops (tomato, potato, pepper, eggplant, tobacco). Many existing studies are stress, tissue, or genotype-specific, which limits cross-species comparisons and interferes with the identification of conserved, stress-responsive metabolic features across the family. Because of the limited spectral libraries and compound annotations, specialised secondary metabolites - particularly alkaloids, phenolics and GAs are poorly resolved. The current studies are based on the metabolic analyses at a single time point in abiotic stress interaction, ignoring the dynamic metabolic reprogramming during stress perception, acclimation and recovery.

Genes and metabolite accumulation cannot be causally inferred because integration with genomics, transcriptomics, proteomics and fluxomics remains uncommon. Furthermore, environmentally realistic stress combinations (e.g. heat-drought, salinity-nutrient stress) and root-shoot metabolite cross-talk remain underexploited still. The lack of standardized experimental designs, metabolite databases specific to Solanaceae and field-level validation limits translational application for breeding abiotic stress-resilient cultivars.

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## Authors' contributions

VDN conceived the idea, designed the study and edited the manuscript. RT, MS and S wrote the first draft of the manuscript. SA formatted the final draft for journal submission. JJ thoroughly reviewed the manuscript. KCS designed the figures. All authors read and approved the final manuscript.

## Compliance with ethical standards

**Conflict of interest:** Authors do not have any conflict of interest to declare.

**Ethical issues:** None

## Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this word, the authors used Napkin AI in order to paraphrase/correct grammatical mistakes and python code generation, respectively. After using this tool/service, the authors reviewed and edited the content as needed and takes full responsibility for the content of the published article.

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